

***COCCINELLA NOVEMNOTATA* IN NORTHEASTERN NORTH AMERICA:
HISTORICAL OCCURRENCE AND CURRENT STATUS
(COLEOPTERA: COCCINELLIDAE)**

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Abstract.—A review of the literature documents that the native lady beetle *Coccinella novemnotata* Herbst (C9) was once common in the northeastern United States and Canada. Despite extensive recent fieldwork and surveys for coccinellids, only five collection records of C9 in the Northeast have been located since the mid-1980s. Its apparent decline in numbers and possible local extirpation could be the result of factors such as changes in land-use and cropping patterns, decline in aphid populations, parasitism, or disease. The factor most often suggested is possible adverse effects from the Old World *C. septempunctata* L. (C7), whose establishment in North America was detected in 1973. New World populations of C7 may have resulted from previous releases for the biological control of aphids or an unintentional importation with commerce. Without a cause-and-effect relationship having been established, proposed detrimental impacts of C7 on native coccinellids are based solely on anecdotal evidence and speculation. Even though C7 was extensively recolonized in North America by biological control specialists, the C7 project does not typify classical biological control. If C7 has had a negative effect on C9, it is more appropriately considered displacement of an indigenous species by a polyphagous nonindigenous species than an example of unintended effects of classical biological control.

Key Words: Insecta, lady beetles, biological control, faunal change

For several years we have realized that the native lady beetle *Coccinella novemnotata* Herbst (hereafter C9) has become increasingly difficult to find in the Northeast and may even be locally extirpated. One hypothesis proposed to account for its apparent decline in numbers is adverse effects from the establishment in North America of a more aggressive congener, the Old World *C. septempunctata* L. (hereafter C7).

In this paper we will demonstrate that *C. novemnotata* was once a widespread and sometimes abundant coccinellid in northeastern North America (Delaware, Maryland, and New Jersey north to Ontario and

Quebec) and that it has been collected only once during surveys and extensive fieldwork in the Northeast in the 1990s. Our intent is (1) to document what others have suspected: that C9 is no longer a common species in the Northeast; (2) to stimulate entomologists, ecologists, and conservation biologists to search for C9 populations in the Northeast and to deposit voucher specimens in major entomological collections; (3) to encourage workers in western North America, where C7 has become established more recently, to begin, or continue, to monitor populations of C9; and (4) to increase interest in documenting the effects of

adventive species—whether intentionally or unintentionally introduced—on indigenous species.

C7 IN NORTH AMERICA

The first U.S. releases of this well-known Old World coccinellid (e.g. Hodek 1973) were made by the U.S. Department of Agriculture (USDA) in California in 1957, based on material from India. Adults were recovered after a month but no further individuals were collected, and no eggs or larvae were observed. From 1958 to 1973, beetles from India, France, Italy, Norway, and Sweden were released (nearly 150,000) for aphid control in eastern and western states by the USDA (Angalet et al. 1979, Schaefer et al. 1987). In eastern Canada small numbers were released in New Brunswick during 1959–1960 (Clark et al. 1971, Schooley et al. 1984). A particular effort was made to establish C7 in Maine for suppression of potato-infesting aphids; about 80,000 individuals were released in test plots at Presque Isle (Shands et al. 1972). Although the F1 generation was recovered at several localities, these releases apparently did not lead to permanent colonization in the United States or Canada (Angalet and Jacques 1975, Angalet et al. 1979, Schaefer et al. 1987).

C7's detection in New Jersey (Angalet and Jacques 1975) and Quebec (Larochelle and Larivière 1979) in 1973 renewed interest in this predator and led to redistribution efforts during 1974–1978 (Angalet et al. 1979). More than 500,000 beetles were released in 20 states and the District of Columbia (Schaefer et al. 1987), and in Canada they were redistributed in Nova Scotia (Kelleher 1984). The beetle's natural dispersal from the area of detection in New Jersey was considered slow: by 1975 records were available only for 10 counties in Connecticut, New Jersey, and New York; its presence in Delaware was considered the result of recolonization (Angalet et al. 1979). But C7's rapid spread began to be documented (Hoe-

beke and Wheeler 1980). Natural spread, aided by successful recolonization in Georgia, Ohio, and Oklahoma, resulted in recoveries from 15 states by the end of 1979 (Schaefer et al. 1987 and references therein).

By 1986, C7 was established in 34 eastern and central states and in 5 Canadian provinces (Schaefer et al. 1987). In Iowa and Missouri this recently established predator was still less abundant than any of the native coccinellids found in croplands, abandoned fields, and roadsides (Obrycki et al. 1987).

Additional releases were planned for the western two-thirds of the United States (Comis and Heppner 1986). Detection of the Russian wheat aphid, *Diuraphis noxia* (Mordvilko), in Texas in 1986 (Stoetzel 1987) further emphasized the need to redistribute C7 in the West (Olkowski et al. 1990, Gordon and Vandenberg 1991). This project was led by the USDA-Animal & Plant Health Inspection Service's National Biological Control Laboratory in Niles, Michigan, and redistribution of C7 in four western states was initiated in 1989 (Flanders et al. 1993). It is now the most commonly collected species of *Coccinella* east of the Rocky Mountains (Gordon and Vandenberg 1991), one of the dominant coccinellids of agricultural crops in Michigan (Maredia et al. 1992), and is known from all 48 contiguous states (Prokrym et al. 1992; see also Rice 1992). In western Canada it occurs in the Prairie Provinces and in central British Columbia (Humble 1991, McNamara 1991). Gene diversity of North American populations is similar to that among Eurasian C7, such a broad genetic basis being characteristic of other successful adventive insects in the New World (Krafsur et al. 1992).

The origin of North American populations of C7 remains in doubt. It was first suspected that the beetles found at the Hackensack Meadowlands in New Jersey were associated with disposal of trash at sites near Kennedy International Airport (Angalet and Jacques 1975). C7's collection in

Quebec, however, suggested separate introductions with transoceanic commerce—along the St. Lawrence Seaway in Quebec and the Upper Bay of the Hudson River and at New Jersey ports of entry (Schaefer et al. 1987). Although an unintentional introduction with ship traffic remains a strong possibility (Schaefer and Dysart 1988, Day et al. 1994), an alternative hypothesis should be considered: that classical biological control releases of C7 made during 1958 to 1973 led to its establishment in the East (Schaefer et al. 1987). Studies of genetic diversity in North American populations have not discriminated between these two hypotheses (Krafsur et al. 1992).

C9 IN NORTH AMERICA

Widespread in North America, this native lady beetle ranges from Maine, Ontario, and Quebec to Florida and west to British Columbia and southern California (Dobzhansky 1931, Gordon 1985) and occurs in all northeastern states (Dobzhansky 1931, Procter 1946, Belicek 1976). In Canada it is found north to 46° in Quebec, 45°30' in Ontario, and 62° in the Northwest Territories (Brown 1962).

Recorded prey includes numerous aphid species (Thompson and Simmonds 1965), and in laboratory evaluations C9 fed more on aphids than on spider mites or lepidopteran eggs (Putman 1957). Larvae and adults similarly preferred aphids to larvae of the alfalfa weevil, *Hypera postica* (Gyllenhal), or leafhopper nymphs (Yadava and Shaw 1968). Although C9 has been considered an important natural enemy of the European corn borer, *Ostrinia nubilalis* (Hübner) (Sparks et al. 1966), more recent work indicates that predation on corn borer eggs is unimportant (Andow 1990). Feeding has also been observed at extrafloral nectaries (Putman 1964, Pemberton and Vandenberg 1993; see also van den Bosch and Telford 1964: Fig. 92).

C9 is especially common in gardens and

other cultivated lands (Leng 1903, Blatchley 1910, Stehr 1930, Chapin 1974, Belicek 1976), occurring in field crops such as alfalfa (Fluke 1925, Goodarzy and Davis 1958, McMullen 1967a, Neuenschwander et al. 1975; see also Hodek 1973), clover (Folsom 1909, Smith 1958), corn (Everly 1938, Bartholomai 1954, Smith 1971, Wright and Laing 1980), cotton (Bell and Whitcomb 1964, Whitcomb and Bell 1964, van den Bosch and Hagen 1966), potatoes (Leonard 1963, Day 1965, Mack and Smilowitz 1980), small grains (Kirk 1970, Shade et al. 1970, Bernal et al. 1993), and soybeans (Blickenstaff and Huggans 1962, Dumas et al. 1964, Tugwell et al. 1973). In Connecticut (Britton 1914) and Minnesota (Stehr 1930), C9 has been ranked as one of the coccinellids of greatest economic importance. C9 can also be collected on weeds in disturbed areas (e.g. McMullen 1967a, Richerson and DeLoach 1973, Dailey et al. 1978, Lago and Mann 1987, Maredia et al. 1992), as well as on apple (Smith 1958, LeRoux 1960, Oatman et al. 1964, Hagley 1975, Travis et al. 1978, Carroll and Hoyt 1984), peach (Putman 1964, Kirk 1970), conifers, and hardwood trees (Felt 1906, Smith 1958, Gagné and Martin 1968, Drooz 1985).

Detailed life history studies of C9 have not been conducted, although Burgess (1903) and Palmer (1914) provided information on fecundity and duration of life stages in the laboratory. Data on preoviposition period, fecundity, and longevity were obtained by McMullen (1967b) and duration of egg and larval stages by Gagné and Martin (1968). Studies on the sex ratio, weight, and size of adults have also been conducted (Smith 1966). Its relative abundance, seasonal history, adult behavior, and factors inducing diapause were studied in California (McMullen 1967a, b). This predator is apparently univoltine in Ontario (Gagné and Martin 1968) and bivoltine in Colorado (Palmer 1914). An important mortality factor may be parasitism by the Holarctic braconid *Dinocampus coccinellae* (Schränk)

(Hudon 1959, Richerson and DeLoach 1973).

Historical occurrence before establishment of C7.—C9 is referred to as frequent throughout Indiana (Blatchley 1910), one of the most abundant coccinellids in Oregon (Ewing 1913), common in Iowa prairies (Hendrickson 1930), and the most common species of *Coccinella* found in Minnesota and the Upper Mississippi Valley (Stehr 1930, Wingo 1952). Occurring statewide in North Carolina (Brimley 1938), South Dakota (Kirk and Balsbaugh 1975), and several northeastern states (see Table 1), C9 is included in many field guides and general references (e.g. Lutz 1948, Jaques 1951, Zim and Cottam 1956, Dillon and Dillon 1961, Swan 1964, Borror and White 1970, Swan and Papp 1972, Milne and Milne 1980, Arnett and Jacques 1981, Arnett 1985, Boyd 1991). In fact, C9 is used as the lead illustration for the coccinellid sections in Arnett (1968) and Borror and White (1970) and in 1989 was designated the official state insect of New York (see Hoffmann and Frodsham 1993). In addition, the USDA's *Cooperative Economic Insect (later Plant Pest) Report* contains numerous references to C9 on various crops. Examples of these state reports include: "Extremely active" on crimson clover, vetch, and cotton in Mobile Co., Alabama (Seibels et al. 1963); "extremely heavy feeding" on woolly apple aphid, *Eriosoma lanigerum* (Hausmann), on apple in Tallapoosa Co., Alabama (Webb et al. 1965); and the most abundant coccinellid in alfalfa (75–100/100 sweeps) in Lafayette Co., Arkansas (Boyer 1970). At one time C9 was routinely collected in the Northeast (Table 1; see also locality records in Dobzhansky 1931).

C9 in the Northeast, 1973–1985.—After C7's detection in North America, C9 continued to be collected in insect surveys in the Northeast during 1973 to 1985. From 1974 to 1978, C9 was scarce at the Hackensack Meadowlands, where C7 had become the dominant coccinellid, and it was also much less numerous than C7 at a near-

by site in Connecticut in 1978 (Angalet et al. 1979; see also Table 2). When C7's establishment was first reported in Pennsylvania, similar numbers of both coccinellids were obtained in limited sweepnet samples (Hoebeke and Wheeler 1980; Table 2). Two years earlier, large numbers of C9 had been found on apple in Pennsylvania (Travis et al. 1978; Table 2).

C9 was not found in surveys of managed, abandoned, and "organic" apple orchards in New York, Pennsylvania, Virginia, and West Virginia during 1983 and 1984, although C7 was present (Brown et al. 1988). Three specimens of C9, however, were collected in Jefferson Co., West Virginia, in 1982, 1984, and 1985 (2 in blacklight traps, 1 in an unsprayed orchard); this species has not since been collected on apple in Jefferson Co. (M. W. Brown, pers. comm. 1994). C9 also was not among the 10 coccinellid species, including C7, collected during a survey of corn insects in the Connecticut Valley of Massachusetts from 1982 to 1984 (Eaton 1984).

C9 in the Northeast since 1985.—We are aware of only five collections of C9 since 1985 (Table 3). One adult was collected at each of two localities in Maryland in 1986 during a survey of coccinellids associated with nursery stock from 1986–1988; C7, however, was taken at 87 of the 186 locations and was the most abundant of the 28 species collected (Staines et al. 1990). C9 has not been seen in Maryland since 1986 (C.L. Staines, Jr., pers. comm. 1994). Populations of the aphid *Cinara pilicornis* (Hartig) were monitored on spruce (*Picea* spp.) seedlings and transplants in a southcentral Pennsylvania nursery during 1987–1988, and two C9 adults were observed on 13 May 1987. But it was C7 that was the most abundant coccinellid associated with aphid-infested spruce (Wheeler 1989 and unpubl. data). In Delaware during a census of overwintering Coccinellidae in a 0.5 ha plot containing >1000 grass clumps, 27 C9 adults were found at Delaware City in winter 1987–

Table 1. Examples of historical occurrence of *Coccinella novemnotata* (C9) in Northeast before establishment of *C. septempunctata* (C7).

State/Province	Remarks	Reference
Connecticut	Common throughout state; of >30 coccinellid spp. recorded, among the 12 considered most economically important	Britton 1914
	Very common at Meriden	Johnson 1915
Maine	Scarce in Mount Desert Region	Procter 1946
Massachusetts	On white birch at Malden, feeding on aphid eggs, 1898	Burgess 1903
	Common on Nantucket Island	Johnson 1930
	Present in cranberry bogs	Franklin 1950
New Jersey	Common throughout state	Smith 1910
	Larvae, adults on <i>Hibiscus moscheutos</i> L.	Weiss and Dickerson 1919
	On <i>Oenothera biennis</i> L., feeding on aphids	Dickerson and Weiss 1920
	On <i>Asclepias syriaca</i> L., <i>A. tuberosa</i> L.	Weiss and Dickerson 1921
New York	Abundant on <i>Pinus rigida</i> Mill. at Karner (Albany Pine Bush)	Felt 1906
	A common species on Staten Island	Leng and Davis 1924
	4th in abundance of 8 coccinellid spp. on alfalfa at Ithaca: 8 adults collected during 10 min. of sampling; one of most abundant coccinellids at Ithaca	Pack 1925
	More localities listed than for any of the other 66 coccinellids recorded from state	Leonard 1928
	Present in small numbers on collards at Ithaca, 1957–1958; 1966–1968	Pimentel 1961, Root 1973
	2nd most numerous coccinellid on potatoes on Long Island, 1956–1958 (19% of family); sometimes abundant late June–early July	Leonard 1963, Day 1965
	On cruciferous crops on Long Island, 1960–1963	Sutherland 1966
	Present in low densities on alfalfa at Ithaca, 1966–1969	Pimentel and Wheeler 1973
	Present in 100-sweep samples of alfalfa in Columbia, Orange, and Steuben counties, May–Aug.; largest number/100 sweeps = 12 in Columbia Co., 15 July 1970	A.G.W., unpublished data
Ontario	Ranked 3rd in abundance among 9 most numerous coccinellid spp. in survey of forages, weeds, and trees; 13% of 2300 specimens collected, 1957	Smith 1958
	Ranked 6th of 10 coccinellid spp. collected, 1948–1960, on peach; 2.9% of 888 specimens identified	Putman 1964
	Represented 19.1% of coccinellids associated with establishment stage of red pine, 1964; numbers dropped drastically in 1965	Gagné and Martin 1968
	Represented 20% of coccinellids (6 spp.) on corn, 1963	Smith 1971
Pennsylvania	Very abundant on oak, feeding on <i>Archips semifera</i> (Walker)	Nichols 1971
Quebec	On apple at Rougemont, 1951–1955 and 1955–1957; predacious on aphids	LeRoux 1960, Parent 1967
	Known historically from 24 localities	Larochelle 1979
Vermont	Known historically from 25 collections	Parker et al. 1976

Table 2. Examples of occurrence of *Coccinella novemnotata* (C9) in Northeast, 1973–1985, after establishment of *C. septempunctata* (C7).

State/Province	Remarks	Reference
Connecticut	16 adults collected (vs. 175 for C7) during survey at Hammonasset, Aug. 1978	Angalet et al. 1979
New Jersey	Scarce at Hackensack Meadowlands, 1974–1978; C7 the most abundant of 17 coccinellid spp. occurring at site	Angalet et al. 1979
Ontario	Common in Pine Barrens On apple at Vineland, 1969–1974 On <i>Onopordum acanthium</i> L., 1976 "Never numerous" in corn, 1977–1978	Boyd and Marucci 1979 Hagley 1975 Judd 1978 Wright and Laing 1980
Pennsylvania	High population levels on apple, 1977; aided significantly in reducing aphid numbers Occasionally common on <i>Euonymus alatus</i> (Thunb.) Sieb. infested with <i>Aphis fabae</i> Scopoli, 1977 10 adults/300 sweeps of weeds in ruderal site (vs. 12 for C7), Harrisburg, 1979 Collected 4 times (vs. 5 for C7) on soybeans, 1980–1982 Larva reared from aphid-infested shoots of <i>Physocarpus opulifolius</i> (L.) Maxim., 1979	Travis et al. 1978 Wheeler and Stimmel 1979 Hoebeke and Wheeler 1980 Wheeler and Stimmel 1983 Wheeler and Hoebeke 1985
Quebec	Collected at 5 localities (vs. 43 for C7), 1979	Larochelle and Larivière 1980
Vermont	On apple in Chittenden Co., 1973–1974	Hauschild 1975

1988; this survey yielded 3000 C7 adults (P. W. Schaefer, pers. comm. 1993). In a study in Maine, C9 was the second most abundant coccinellid (C7 was most abundant) found in potato plots and the second most numerous lady beetle in barley plots adjacent to potato in 1992. C9 was not encountered in either crop in 1993 (F. A. Drummond, pers. comm. 1994), which could reflect normal year-to-year fluctuations in density rather than an actual decline in numbers.

No detections of C9 were made in the Northeast during 1993 coccinellid surveys conducted as part of the USDA's Cooperative Agricultural Pest Survey program. In Connecticut, an alfalfa field in each of 4 counties was sampled 6 times (400 sweeps/visit) from 10 June to 19 August and once in September; supplemental 200-sweep samples were taken at 16 sites in 4 counties during June to September (D. Ellis, pers. comm. 1993). New York surveys consisted of 1500 sweeps taken 4–5 times in alfalfa

or clover fields in each of 4 counties (1 was sampled only 3 times) from 15 July to 9 September; additional samples from forages and goldenrod were taken in 5 counties during August and September (J. J. Knodel, pers. comm. 1993). In Pennsylvania, 3 alfalfa fields in 3 counties were each monitored 6 times (400 sweeps/visit) from 18 June to 1 September; 52 additional fields or disturbed weedy sites were surveyed in 18 counties from June to August. Similar coccinellid surveys in various disturbed habitats in Pennsylvania (136 sites in 23 eastern counties) were also negative for C9 in 1994 (A.G.W., unpubl. data).

Moreover, C9 was not observed during an extensive survey for the adventive *Hippodamia variegata* (Goeze) in the Northeast in 1992. Nearly 600 adults of 8 coccinellid species, including 66 C7, were collected in 8 states (Wheeler 1993). We have not seen C9 in general collecting since 1985 or in our surveys of disturbed and relatively undisturbed habitats ranging from urban vacant

Table 3. Known records of *Coccinella novemnotata* (C9) in Northeast since 1985; see text for additional information on collections.

State	Remarks	Reference
Delaware	27 adults at Delaware City, winter 1987–1988	P. W. Schaefer, pers. comm.
Maine	Common on barley and potatoes in study plots at Presque Isle, 1992	F. A. Drummond, pers. comm.
Maryland	Two collections during 1986–1988: 1 adult on nursery stock in Allegany Co., another in Carroll Co.	Staines et al. 1990
Pennsylvania	Two adults on spruce transplants in Cumberland Co. nursery, May 1987	Wheeler 1989, unpubl. data

lots to pitch pine-scrub oak barrens, serpentine barrens, and shale barrens. No recent records of C9 were available in the insect collections that were checked: American Museum of Natural History, New York; Canadian National Collection, Ottawa; Carnegie Museum of Natural History, Pittsburgh; Cornell University, Ithaca, N.Y.; Florida State Collection of Arthropods, Gainesville; National Museum of Natural History, Washington, D.C.; Ohio State University, Columbus; Pennsylvania State University, University Park; University of Maine, Orono; and University of New Hampshire, Durham.

DISCUSSION

Adverse effects from the establishment of C7 is only one possible explanation for the apparent decline in C9 populations. Other factors that could be involved are changes in land-use and cropping patterns, decline in aphid densities, parasitism, disease, or even global warming. It is C7, however, that has been proposed most often as the likely cause of C9's decline.

Soon after C7's establishment in eastern North America, its possible detrimental effects on native coccinellids began to be noted. There was no evidence for C7's replacement of native coccinellids in Georgia within three years of its release and establishment for suppression of pecan aphids (Teddners and Angalet 1981), but by the early 1980s a possible "antagonistic relationship with *C. novemnotata* appeared to be

developing" in Ontario (W. Y. Watson, letter to A.G.W., 11 Feb. 1983). The need to evaluate the effects of the rapidly spreading C7 on the native coccinellid fauna became apparent (Schaefer et al. 1987). When field surveys were conducted during a three-year period in Maryland (186 localities), the once "very common" C9 was collected only twice. Competitive displacement by C7 was suggested as a reason for the apparent diminished numbers of C9 in Maryland (Staines et al. 1990). Ehler (1990) also emphasized C7's potential for affecting nontarget species (see also Evans 1991, Tedders 1992, Elliott et al. 1993, and Wheeler 1993). The seven-spotted lady beetle's possible effects on endangered lycaenid butterflies have recently been evaluated in Ohio. Although their population declines coincided with increases in C7 and this coccinellid fed on lycaenid eggs in the laboratory (Horn 1991), no field data are available to substantiate any adverse effect of C7 on these endangered lepidopterans.

Populations of C9 in the Northeast seem to have declined sharply during the 1980s and 1990s, a period when the Old World C7 was undergoing rapid range expansion. Our after-the-fact evidence for the adverse effects of C7 on C9 must be considered circumstantial. Populations of C9 were not monitored systematically during the time when C7 was becoming established in the Northeast and assuming dominance among coccinellids in disturbed and relatively undisturbed communities. Coccinellid densi-

ties often fluctuate widely from year to year (e.g. Foott 1974, Elliott and Kieckhefer 1990, Kieckhefer and Elliott 1990, Elliott et al. 1993). Quantitative data from sampling at several sites over a 10- to 15-year period—beginning even before the establishment of C7 in the local fauna—would therefore be needed to assess accurately C7's role among various other factors that may be responsible for a decline in populations of C9.

Except in classical biological control of weeds programs, rarely are such quantified data available assessing the effects of adventive species on indigenous organisms; however, there are incomplete baseline data documenting the presence and abundance of C9. Literature references adequately support the view that C9 was once routinely collected or observed in the Northeast, often in considerable numbers. If C9 were still relatively common, it should have been detected during recent surveys for Old World coccinellids in the Northeast or in our extensive fieldwork involving agricultural crops, herbaceous weeds, shrubs, and trees since 1987. Adults of C9 are conspicuous because of their size (Britton 1914). Even though adults somewhat resemble those of C7, the two species are easily recognized. The head of C9 has a solid white rectangle instead of two white dots, and the anterior pronotal margin has a narrow white border, which is lacking in C7. C9's recognition in the East is not complicated by the pronounced color polymorphism that characterizes certain native or naturalized lady beetles in our fauna; only the fully maculate nine-spotted morph occurs in eastern North America (Belicek 1976, Gordon and Vandenberg 1991). As evidence for a recent decline in C9 populations, data from extensive fieldwork probably should be weighted more heavily than the absence of new material in collections (museum accessions sometimes are not processed for several years).

The sevenspotted lady beetle is a voracious, nearly ubiquitous aphidophage in the

Old World that can also be characterized as eurytopic, polyphagous, and ecologically plastic (Hodek 1973). The aggressive adults (see Miller 1992) will attack early-instar chrysopid larvae, even when other prey are available (Şengonca and Frings 1985). For a summary of studies on its foraging behavior, see Kareiva (1986) and Andersen and Kareiva (1993). C7 is an active flier and an aggressive colonizer that has become established on Sable Island, Nova Scotia, which is isolated in the Atlantic about 175 km from the nearest land (Schaefer et al. 1987), and also at high elevations (nearly 3500 m) in the Rocky Mountains (Rice 1992).

The only evidence available that C9 might be susceptible to interspecific competition is the possibility that its gradual disappearance from establishment-stage red pine in Ontario was the result of competition from other coccinellids (Gagné and Martin 1968). Competitive displacement and interspecific predation by C7, as well as pesticide use and changes in land management, could contribute to declining populations of C9 in the Northeast. Determining the precise nature of C7's detrimental effects on C9 would prove difficult.

C7's explosive colonization of North America provides an opportunity for evaluating the effects of an aggressive polyphagous predator on nontarget organisms. Ehler (1990) found "it difficult to believe that this introduction will not have an impact on non-target species in the United States," and Evans (1991) suggested that C7 "may have profound impact on the ladybeetle fauna native to North America through complex interactions of Old and New World ladybeetles." Indeed, uncommon coccinellids temporarily disappeared from cropfields in South Dakota following the invasion and establishment of C7 (Elliott et al. 1993), although C7 was not shown to be a direct cause of their decline; factors other than C7's establishment could be involved.

C9 is still common in parts of western

North America. In fact, its relatively high densities (and those of *Hippodamia convergens* Guérin-Ménéville) may have hindered or delayed C7's establishment in California (Flanders et al. 1993). At most, C9 may be only locally extirpated in the East. Workers in the Northeast and even the Southeast (C9 appears at least to have declined in Alabama and Mississippi during the past five years; P. M. Estes and R. L. Brown, pers. comm. 1994, 1995) are encouraged to look for this native species. Workers in areas where C7 is a more recent invader may want to begin, or continue (Elliott et al. 1993), to monitor its potential effects on C9 and other native coccinellids, as well as document a decline in populations of injurious aphids (see Kauffman and Schwalbe 1991). There is also a need to determine if other recently established Eurasian lady beetles—*Harmonia axyridis* (Pallas), *Hippodamia variegata*, and *Propylea quatuordecimpunctata* L.—are affecting native coccinellids in the East (see Day et al. 1994).

Most people will not be concerned if an introduced predator having superior attributes reduces pest populations more than do indigenous natural enemies. So many plant and animal species have been affected by the needs of human society (e.g. Soulé 1990) that a decline in numbers of one or a few native predators will be viewed as inconsequential. Local extirpation or extinction of C9 would elicit more concern.

It is likely that C9 will find habitats in which it can coexist with C7; such populations, as yet undetected, may exist in the Northeast. Its populations may again build to sizable levels. The current low densities of C9 in the Northeast may actually be similar to those that existed before the advent of agroecosystems, which facilitated increases in aphid numbers, allowing C9 perhaps to reach population levels greater than before human intervention.

The benefits of C7's presence in the Neartic fauna may outweigh any costs to the environment. Use of pesticides against an

important crop pest may actually pose more of an environmental threat than does the release of some biological control agent (e.g. Nechols et al. 1992). The establishment of C7 can be viewed as representing a continuum of ecological changes. We have discussed C7 as a principal factor contributing to a decline in populations of C9, although the evidence is speculative and anecdotal. But C7 may even be having positive effects on other nontarget organisms.

The importation of any biological control agent is an experiment. Most introduced species fail to become established, relatively few provide substantial suppression of target pests, and fewer still cause serious environmental problems (e.g. Hall and Ehler 1979, Hall et al. 1980, Samways 1988, Ehler 1990). Whether any environmental disruption associated with C7's establishment is considered acceptable should await the results of long-term ecological monitoring, preferably at sites where C7 and C9 do and do not co-occur, and critical evaluation of the accumulated quantitative data. Even then, an evaluation of the program to recolonize C7 in North America will be influenced by one's environmental, political, and social views.

SUMMARY AND CONCLUSIONS

Classical biological control has traditionally been favorably received by conservationists and environmentalists (Samways 1988) but is under increasing pressure from such groups (Howarth 1983, 1991, Nechols and Kauffman 1992, Simberloff 1992, Lockwood 1993, Miller and Aplet 1993, U.S. Congress 1993). We realize the introduction of biological control agents has been viewed as part of the larger problem of environmental disruption resulting from invasion of nonindigenous species (Howarth 1983, 1991, Samways 1988, Ehler 1990, 1991, Miller and Aplet 1993). Moreover, we support the need to analyze and evaluate biological control projects, but the data used and conclusions reached should have a

sound scientific basis and avoid inference and speculation.

We cannot document a cause-and-effect relationship between the establishment of C7 and the decline of C9. What can be stated with reasonable certainty is that C7 has increased and, at the same time and in some of the same places, C9 has decreased. Proposed adverse effects of C7 on native coccinellids, such as *Hippodamia convergens* (Teddars 1992) and *C. transversoguttata richardsoni* Brown, are now based entirely on speculation.

That all forms of pest control—biological as well as chemical—pose some environmental risk is well known (Taylor 1955, Elton 1958, Turnbull and Chant 1961, Ehler and van den Bosch 1974, Beirne 1975, Pimentel et al. 1984, Carruthers and Onsager 1993, Drea 1993, Miller and Aplet 1993). Consequently, biological control practitioners generally, especially those involved with weeds, have attempted to minimize potential environmental problems (e.g. Zwölfer and Harris 1971, Harris 1973, Goeden 1983, Klingman and Coulson 1983).

It is tempting to look at the case of C7 and C9 within the context of classical biological control. Even though C7 was recolonized extensively by biological control specialists, this project does not typify classical biological control. Initially there was no target pest (e.g. Comis and Heppner 1986); only later was the Russian wheat aphid identified as the target aphid for redistribution. It is also uncertain whether the successful invasive genotype of C7 should be attributed to intentional releases in North America or to an accidental introduction with commerce. If C7 has indeed adversely affected C9, that interaction is more appropriately viewed as displacement of an indigenous species by a polyphagous, aggressive nonindigenous species. It should not be cited as an example of negative effects of classical biological control. Instead it reemphasizes the continuing need to assess host (and prey) specificity of all agents consid-

ered for release in classical biological control programs.

ACKNOWLEDGMENTS

We are grateful to M. W. Brown, F. A. Drummond, D. Ellis, P. M. Estes, J. J. Knodel, R. L. Brown, P. W. Schaefer, C. L. Staines, Jr., and W. Y. Watson for allowing us to refer to their unpublished data or correspondence; E. C. Becker, S. W. Bullington, D. S. Chandler, J. R. Coulson, W. H. Day, L. E. Ehler, R. D. Gordon, K. I. Hauschild, L. A. Hull, W. C. Kauffman, J. V. McHugh, R. Mack, J. J. Obrycki, S. C. Passoa, T. M. Peters, P. E. Skelley, W. L. Tedders, and M. C. Thomas for checking collections or files for records of *C. novemnotata* or providing copies of papers; R. L. Stewart and C. A. Stoops for helping survey for coccinellids in Pennsylvania during 1993–1994; and E. S. Delfosse, L. E. Ehler, J. H. Frank, J. C. Miller, J. J. Obrycki, and R. L. Pienkowski for useful comments on the manuscript.

LITERATURE CITED

- Andersen, M. and P. M. Kareiva. 1993. Interactions between imported predators and their prey in patchy environments, pp. 243–258. In Kim, K. C. and B. A. McPheron, eds., *Evolution of Insect Pests: Patterns of Variation*. John Wiley & Sons, New York.
- Andow, D. A. 1990. Characterization of predation on egg masses of *Ostrinia nubilalis* (Lepidoptera: Pyralidae). *Annals of the Entomological Society of America* 83: 482–486.
- Angalet, G. W. and R. L. Jacques. 1975. The establishment of *Coccinella septempunctata* L. in the continental United States. United States Department of Agriculture, Cooperative Economic Insect Report 25(45–48): 883–884.
- Angalet, G. W., J. M. Tropp, and A. N. Eggert. 1979. *Coccinella septempunctata* in the United States: recolonizations and notes on its ecology. *Environmental Entomology* 8: 896–901.
- Arnett, R. H., Jr. 1968. *The Beetles of the United States (A Manual for Identification)*. American Entomological Institute, Ann Arbor, Mich. 1112 pp.
- Arnett, R. H., Jr. 1985. *American Insects: A Handbook of the Insects of America North of Mexico*. Van Nostrand Reinhold, New York. 850 pp.
- Arnett, R. H., Jr. and R. L. Jacques, Jr. 1981. Simon

- and Schuster's Guide to Insects. Simon and Schuster, New York. 511 pp.
- Bartholomai, C. W. 1954. Predatism of European corn borer eggs by arthropods. *Journal of Economic Entomology* 47: 295-299.
- Beirne, B. P. 1975. Biological control attempts by introductions against pest insects in the field in Canada. *Canadian Entomologist* 107: 225-236.
- Belicek, J. 1976. Coccinellidae of western Canada and Alaska with analyses of the transmontane zoogeographic relationships between the fauna of British Columbia and Alberta (Insecta: Coleoptera: Coccinellidae). *Quaestiones Entomologicae* 12: 283-409.
- Bell, K. O. and W. H. Whitcomb. 1964. Field studies on egg predators of the bollworm, *Heliothis zea* (Boddie). *Florida Entomologist* 47: 171-180.
- Bernal, J., D. González, E. T. Natwick, J. G. Loya, R. León-Lopez, and W. E. Bendixen. 1993. Natural enemies of Russian wheat aphid identified in California. *California Agriculture* 47(6): 24-28.
- Blickenstaff, C. C. and J. L. Huggans. 1962. Soybean insects and related arthropods in Missouri. University of Missouri Agricultural Experiment Station Research Bulletin 803. 51 pp.
- Blatchley, W. S. 1910. An Illustrated Descriptive Catalogue of the Coleoptera or Beetles (Exclusive of the Rhynchophora) Known to Occur in Indiana. Nature Publishing, Indianapolis. 1386 pp.
- Borrer, D. J. and R. E. White. 1970. A Field Guide to the Insects of America North of Mexico. Houghton Mifflin, Boston. 404 pp.
- Boyd, H. P. 1991. A Field Guide to the Pine Barrens of New Jersey: Its Flora, Fauna, Ecology and Historic Sites. Plexus Publishing, Medford, N.J. 423 pp.
- Boyd, H. P. and P. E. Marucci. 1979. Arthropods of the Pine Barrens, pp. 505-525. In Forman, R. T. T., ed., *Pine Barrens: Ecosystem and Landscape*. Academic Press, New York.
- Boyer, W. P. 1970. Lady beetles—ARKANSAS. United States Department of Agriculture, Cooperative Economic Insect Report 20(20): 329.
- Brimley, C. S. 1938. The Insects of North Carolina. North Carolina Department of Agriculture, Raleigh. 560 pp.
- Britton, W. E. 1914. Some common lady beetles of Connecticut. *Connecticut Agricultural Experiment Station Bulletin* 181. 24 pp.
- Brown, M. W., C. R. L. Adler, and R. W. Weires. 1988. Insects associated with apple in the mid-Atlantic states. *New York's Food and Life Sciences Bulletin* 124.31 pp.
- Brown, W. J. 1962. A revision of the forms of *Coccinella* L. occurring in America north of Mexico (Coleoptera: Coccinellidae). *Canadian Entomologist* 94: 785-808.
- Burgess, A. F. 1903. Economic notes on the family Coccinellidae. United States Department of Agriculture, Division of Entomology Bulletin 40(N.S.), pp. 25-29.
- Carroll, D. P. and S. C. Hoyt. 1984. Natural enemies and their effects on apple aphid, *Aphis pomi* DeGeer (Homoptera: Aphididae), colonies on young apple trees in central Washington. *Environmental Entomology* 13: 469-481.
- Carruthers, R. I. and J. A. Onsager. 1993. Perspective on the use of exotic natural enemies for biological control of pest grasshoppers (Orthoptera: Acrididae). *Environmental Entomology* 22: 885-903.
- Chapin, J. B. 1974. The Coccinellidae of Louisiana (Insecta: Coleoptera). Louisiana Agricultural Experiment Station Bulletin 682. 87 pp.
- Clark, R. C., D. O. Greenbank, D. G. Bryant, and J. W. E. Harris. 1971. *Adelges piceae* (Ratz.), balsam woolly aphid (Homoptera: Adelgidae), pp. 113-127. In Corbet, P. S. and R. M. Prentice, compilers, *Biological Control Programmes against Insects and Weeds in Canada 1959-1968*. Commonwealth Institute of Biological Control, Trinidad. Technical Communication 4.
- Comis, D. and M. Heppner. 1986. Battle for national assault on aphids. *Agricultural Research* (Washington, D.C.) 34(6): 10-12.
- Dailey, P. J., R. C. Graves, and J. M. Kingsolver. 1978. Survey of Coleoptera collected on the common milkweed, *Asclepias syriaca*, at one site in Ohio. *Coleopterists Bulletin* 32: 223-229.
- Day, W. H. 1965. The identification and importance of biotic and abiotic factors affecting aphids on Long Island potatoes. Ph.D. thesis, Cornell University, Ithaca, N.Y. 420 pp.
- Day, W. H., D. R. Prokrym, D. R. Ellis, and R. J. Chianese. 1994. The known distribution of the predator *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae) in the United States, and thoughts on the origin of this species and five other exotic lady beetles in eastern North America. *Entomological News* 105: 244-256.
- Dickerson, E. L. and H. B. Weiss. 1920. The insects of the evening primroses in New Jersey. *Journal of the New York Entomological Society* 28: 32-74.
- Dillon, E. S. and L. S. Dillon. 1961. *A Manual of Common Beetles of Eastern North America*. Row, Peterson and Co., Evanston, Ill. 884 pp.
- Dobzhansky, T. 1931. The North American beetles of the genus *Coccinella*. *Proceedings of the United States National Museum* 80(4): 1-32.
- Drea, J. J. 1993. Classical biological control—an endangered discipline?, pp. 215-222. In McKnight, B. N., ed., *Biological Pollution: The Control and Impact of Invasive Exotic Species*. Indiana Academy of Science, Indianapolis.
- Drooz, A. T., ed. 1985. *Insects of Eastern Forests*. U.S. Department of Agriculture, Forest Service.

- Miscellaneous Publication 1426. U.S. Government Printing Office, Washington, D.C. 608 pp.
- Dumas, B. A., W. P. Boyer, and W. H. Whitcomb. 1964. Effect of various factors on surveys of predaceous insects in soybeans. *Journal of the Kansas Entomological Society* 37: 192-201.
- Eaton, D. M. 1984. The insect fauna of field corn in Massachusetts. M.S. Research Project, University of Massachusetts, Amherst. 21 pp.
- Ehler, L. E. 1990. Environmental impact of introduced biological-control agents: Implications for agricultural biotechnology, pp. 85-96. *In* Marois, J. J. and G. Bruening, eds., *Risk Assessment in Agricultural Biotechnology: Proceedings of the International Conference*. University of California Division of Agriculture and Natural Resources, Publication 1928.
- Ehler, L. E. 1991. Planned introductions in biological control, pp. 21-39. *In* Ginzburg, L. R., ed., *Assessing Ecological Risks of Biotechnology*. Butterworth-Heinemann, Boston.
- Ehler, L. E. and R. van den Bosch. 1974. An analysis of the natural biological control of *Trichoplusia ni* (Lepidoptera: Noctuidae) on cotton in California. *Canadian Entomologist* 106: 1067-1073.
- Elliott, N. C. and R. W. Kieckhefer. 1990. Dynamics of aphidophagous coccinellid assemblages in small grain fields in eastern South Dakota. *Environmental Entomology* 19: 1320-1329.
- Elliott, N. C., R. W. Kieckhefer, and W. C. Kauffman. 1993. Effects of an invading coccinellid, *Coccinella septempunctata* L., on the structure of native coccinellid species assemblages in agricultural crops. *Bulletin of the Ecological Society of America* 74(2 suppl.): 226.
- Elton, C. S. 1958. *The Ecology of Invasions by Animals and Plants*. Methuen, London. 181 pp.
- Evans, E. W. 1991. Intra versus interspecific interactions of ladybeetles (Coleoptera: Coccinellidae) attacking aphids. *Oecologia* 87: 401-408.
- Everly, R. T. 1938. Spiders and insects found associated with sweet corn with notes on the food and habits of some species. I. Arachnida and Coleoptera. *Ohio State Journal of Science* 38: 136-148.
- Ewing, H. E. 1913. Notes on Oregon Coccinellidae. *Journal of Economic Entomology* 6: 404-407.
- Felt, E. P. 1906. *Insects Affecting Park and Woodland Trees*. Vol. 2. New York State Museum Memoir 8, pp. 333-877. New York State Education Department, Albany.
- Flanders, R. V., D. J. Nelson, C. J. Copeland, and W. Weitsen. 1993. Russian wheat aphid biological control project: FY 1991 project report. U.S. Department of Agriculture, National Biological Control Laboratory, Niles, Mich. 56 pp.
- Fluke, C. L., Jr. 1925. Natural enemies of the pea aphid (*Illinoia pisi* Kalt.); their abundance and distribution in Wisconsin. *Journal of Economic Entomology* 18: 612-616.
- Folsom, J. W. 1909. The insect pests of clover and alfalfa, pp. 41-124. *In* Forbes, S. A., ed., *Twenty-fifth Report of the State Entomologist on the Noxious and Beneficial Insects of the State of Illinois*, Urbana, Ill.
- Foott, W. H. 1974. Observations on Coccinellidae in corn fields in Essex County, Ontario. *Proceedings of the Entomological Society of Ontario* 104: 16-21.
- Franklin, H. J. 1950. Cranberry insects in Massachusetts. Parts II-VII. *Massachusetts Agricultural Experiment Station Bulletin* 445 (cont.). 88 pp.
- Gagné, W. C. and J. L. Martin. 1968. The insect ecology of red pine plantations in central Ontario. V. The Coccinellidae (Coleoptera). *Canadian Entomologist* 100: 835-846.
- Goeden, R. D. 1983. Critique and revision of Harris' scoring system for selection of insect agents in biological control of weeds. *Protection Ecology* 5: 287-301.
- Goodarzy, K. and D. W. Davis. 1958. Natural enemies of the spotted alfalfa aphid in Utah. *Journal of Economic Entomology* 51: 612-616.
- Gordon, R. D. 1985. The Coccinellidae (Coleoptera) of America north of Mexico. *Journal of the New York Entomological Society* 93: 1-912.
- Gordon, R. D. and N. Vandenberg. 1991. Field guide to recently introduced species of Coccinellidae (Coleoptera) in North America, with a revised key to North American genera of Coccinellini. *Proceedings of the Entomological Society of Washington* 93: 845-864.
- Hagley, E. A. C. 1975. The arthropod fauna in unsprayed apple orchards in Ontario II. Some predacious species. *Proceedings of the Entomological Society of Ontario* 105: 28-40.
- Hall, R. W. and L. E. Ehler. 1979. Rate of establishment of natural enemies in classical biological control. *Bulletin of the Entomological Society of America* 25: 280-282.
- Hall, R. W., L. E. Ehler, and B. Bisabri-Ershadi. 1980. Rate of success in classical biological control of arthropods. *Bulletin of the Entomological Society of America* 26: 111-114.
- Harris, P. 1973. The selection of effective agents for the biological control of weeds. *Canadian Entomologist* 105: 1495-1503.
- Hauschild, K. I. 1975. *Lygus lineolaris* in apple orchards in Vermont: A population study with reference to selected arthropod predators. M.S. thesis, University of Vermont, Burlington. 75 pp.
- Hendrickson, G. O. 1930. Studies on the insect fauna of Iowa prairies. *Iowa State College Journal of Science* 4: 49-179.
- Hodek, I. 1973. *Biology of Coccinellidae*. Dr. W.

- Junk Publishers, The Hague; Academia, Prague. 260 pp.
- Hoebeke, E. R. and A. G. Wheeler, Jr. 1980. New distribution records of *Coccinella septempunctata* L. in the eastern United States (Coleoptera: Coccinellidae). *Coleopterists Bulletin* 34: 209–212.
- Hoffmann, M. P. and A. C. Frodsham. 1993. *Natural Enemies of Vegetable Insect Pests*. Cornell Cooperative Extension Publication, Ithaca, N.Y. 63 pp.
- Horn, D. J. 1991. Potential impact of *Coccinella septempunctata* on endangered Lycaenidae (Lepidoptera) in northwestern Ohio, USA, pp. 159–162. In Polgár, L., R. J. Chambers, A. F. G. Dixon, and I. Hodek, eds., *Behaviour and Impact of Aphidophaga*. SPB Academic Publishing, The Hague.
- Howarth, F. G. 1983. Classical biocontrol: panacea or Pandora's box. *Proceedings of the Hawaiian Entomological Society* 24: 239–244.
- Howarth, F. G. 1991. Environmental impacts of classical biological control. *Annual Review of Entomology* 36: 485–509.
- Hudon, M. 1959. First record of *Perilitus coccinellae* (Schrank) (Hymenoptera: Braconidae) as a parasite of *Coccinella novemnotata* Hbst. and *Coleomegilla maculata lengi* Timb. (Coleoptera: Coccinellidae) in Canada. *Canadian Entomologist* 91: 63–64.
- Humble, L. M. 1991. Occurrence of *Coccinella septempunctata* (L.) (Coleoptera: Coccinellidae) in central British Columbia. *Pan-Pacific Entomologist* 67: 224–226.
- Jaques, H. E. 1951. *How to Know the Beetles*. Wm. C. Brown, Dubuque, Iowa. 372 pp.
- Johnson, C. W. 1930. A list of the insect fauna of Nantucket, Massachusetts. *Publications of the Nantucket Maria Mitchell Association* 3(2): 1–174.
- Johnson, H. L. 1915. Coleoptera found in the vicinity of Meriden, Connecticut. *Entomological News* 26: 307–319.
- Judd, W. W. 1978. Insects associated with a colony of aphids, *Brachycaudus cardui* L., on Scotch thistle, *Onopordum acanthium* L., at Dunnville, Ontario. *Entomological News* 89: 169–173.
- Kareiva, P. 1986. Patchiness, dispersal, and species interactions: Consequences for communities of herbivorous insects, pp. 192–206. In Diamond, J. and T. J. Case, eds., *Community Ecology*. Harper & Row, New York.
- Kauffman, W. C. and C. P. Schwalbe. 1991. Plant growth responses to *Aphis fabae* injury: Importance of predation by *Coccinella septempunctata* (Coleoptera: Coccinellidae), pp. 167–175. In Polgár, L., R. J. Chambers, A. F. G. Dixon, and I. Hodek, eds., *Behaviour and Impact of Aphidophaga*. SPB Academic Publishing, The Hague.
- Kelleher, J. S. 1984. Current approaches to biological control of agricultural insect pests, pp. 3–5. In Kelleher, J. S. and M. A. Hulme, eds., *Biological Control Programmes against Insects and Weeds in Canada 1969–1980*. Commonwealth Agricultural Bureaux, Farnham Royal, Slough, England.
- Kieckhefer, R. W. and N. C. Elliott. 1990. A 13-year survey of the aphidophagous Coccinellidae in maize fields in eastern South Dakota. *Canadian Entomologist* 122: 579–581.
- Kirk, V. M. 1970. A list of the beetles of South Carolina. Part 2-Mountain, piedmont, and southern coastal plain. *South Carolina Agricultural Experimental Station Technical Bulletin* 1038. 117 pp.
- Kirk, V. M. and E. U. Balsbaugh, Jr. 1975. A list of the beetles of South Dakota. *South Dakota State University Agricultural Experiment Station Technical Bulletin* 42. 139 pp.
- Klingman, D. L. and J. R. Coulson. 1983. Guidelines for introducing foreign organisms into the United States for the biological control of weeds. *Bulletin of the Entomological Society of America* 29(3): 55–61.
- Krafsur, E. S., J. J. Obrycki, and R. V. Flanders. 1992. Gene flow in populations of the seven-spotted lady beetle, *Coccinella septempunctata*. *Journal of Heredity* 83: 440–444.
- Lago, P. K. and M. O. Mann. 1987. Survey of Coleoptera associated with flowers of wild carrot (*Daucus carota* L.) (Apiaceae) in northern Mississippi. *Coleopterists Bulletin* 41: 1–8.
- Larochelle, A. 1979. Les Coléoptères Coccinellidae du Québec. *Cordulia*, Supplement 10: 1–111.
- Larochelle, A. and M.-C. Larivière. 1979. *Coccinella septempunctata* L. (Coleoptera: Coccinellidae) au Québec: répartition géographique, habitat et biologie. *Bulletin d'Inventaire des Insectes du Québec* 1(4): 68–76.
- . 1980. Capture de Coleopteres Coccinellidae au Québec en 1979. *Bulletin d'Inventaire des Insectes du Québec* 2(2): 21–35.
- Leng, C. W. 1903. Notes on Coccinellidae.—II. *Journal of the New York Entomological Society* 11: 193–213.
- Leng, C. W. and W. T. Davis. 1924. List of the Coleoptera of Staten Island, New York. *Proceedings of the Staten Island Institute of Arts and Sciences* 2(1): 1–82.
- Leonard, M. D., ed. 1928. A list of the insects of New York with a list of the spiders and certain other allied groups. *Cornell University Agricultural Experiment Station Memoir* 101. 1121 pp.
- Leonard, M. D. 1963. A list of aphids of New York. *Proceedings of the Rochester Academy of Science* 10: 289–428.
- LeRoux, E. J. 1960. Effects of "modified" and "commercial" spray programs on the fauna of apple

- orchards in Quebec. *Annales de la Société Entomologique du Québec* 6: 87-121.
- Lockwood, J. A. 1993. Environmental issues involved in biological control of rangeland grasshoppers (Orthoptera: Acrididae) with exotic agents. *Environmental Entomology* 22: 503-518.
- Lutz, F. E. 1948. *Field Book of Insects of the United States and Canada, Aiming to Answer Common Questions*, 3rd ed. rev. G. P. Putnam's Sons, New York. 510 pp.
- Mack, T. P. and Z. Smilowitz. 1980. The development of a green peach aphid natural enemy sampling procedure. *Environmental Entomology* 9: 440-445.
- McMullen, R. D. 1967a. A field study of diapause in *Coccinella novemnotata* (Coleoptera: Coccinellidae). *Canadian Entomologist* 99: 42-49.
- McMullen, R. D. 1967b. The effects of photoperiod, temperature, and food supply on rate of development and diapause in *Coccinella novemnotata*. *Canadian Entomologist* 99: 578-586.
- McNamara, J. 1991. Family Coccinellidae, ladybird beetles, pp. 229-237. In Bousquet, Y., ed., *Checklist of Beetles of Canada and Alaska*. Research Branch Agriculture Canada Publication 1861/E. Minister of Supply and Services Canada, Ottawa.
- Maredia, K. M., S. H. Gage, D. A. Landis, and T. M. Wirth. 1992. Ecological observations on predatory Coccinellidae (Coleoptera) in southwestern Michigan. *Great Lakes Entomologist* 25: 265-270.
- Miller, J. C. 1992. Coccinellid research in the Pacific Northwest. *Ladybeetle Flyer* 6: 4.
- Miller, M. and G. Aplet. 1993. Biological control: A little knowledge is a dangerous thing. *Rutgers Law Review* 45: 285-334.
- Milne, L. and M. Milne. 1980. *The Audubon Society Field Guide to North American Insects and Spiders*. Alfred A. Knopf, New York. 989 pp.
- Nechols, J. R. and W. C. Kauffman. 1992. Introduction and overview, pp. 1-5. In Kauffman, W. C. and J. R. Nechols, eds., *Selection Criteria and Ecological Consequences of Importing Natural Enemies*. Thomas Say Publications in Entomology: Proceedings. Entomological Society of America, Lanham, Md.
- Nechols, J. R., W. C. Kauffman, and P. W. Schaefer. 1992. Significance of host specificity in classical biological control, pp. 41-52. In Kauffman, W. C. and J. R. Nechols, eds., *Selection Criteria and Ecological Consequences of Importing Natural Enemies*. Thomas Say Publications in Entomology: Proceedings. Entomological Society of America, Lanham, Md.
- Neuenschwander, P., K. S. Hagen, and R. F. Smith. 1975. Predation on aphids in California's alfalfa fields. *Hilgardia* 43: 53-78.
- Nichols, [J. O.]. 1971. A tortricid moth (*Archips semiferanus*). United States Department of Agriculture, Cooperative Economic Insect Report 21(28): 494.
- Oatman, E. R., E. F. Legner, and R. F. Brooks. 1964. An ecological study of arthropod populations on apple in northeastern Wisconsin. *Journal of Economic Entomology* 57: 978-983.
- Obrycki, J. J., W. C. Bailey, C. R. Stoltene, B. Puttler, and C. E. Carlson. 1987. Recovery of the seven-spotted lady beetle, *Coccinella septempunctata* (Coleoptera: Coccinellidae), in Iowa and Missouri. *Journal of the Kansas Entomological Society* 60: 584-588.
- Olkowski, W., A. Zhang, and P. Thiers. 1990. Improved biocontrol techniques with lady beetles. *IPM Practitioner* 12(10): 1-12.
- Pack, H. J. 1925. A biological study of certain ladybird beetles (Coccinellidae). Ph.D. thesis, Cornell University, Ithaca, N.Y. 157 pp.
- Palmer, M. A. 1914. Some notes on life history of ladybeetles. *Annals of the Entomological Society of America* 7: 213-238.
- Parent, B. 1967. Population studies of phytophagous mites and predators on apple in southwestern Quebec. *Canadian Entomologist* 99: 771-778.
- Parker, B. L., G. R. Nielsen, and R. T. Bell. 1976. Lady beetles: a checklist of the Coccinellidae of Vermont (Insecta: Coleoptera). University of Vermont Agricultural Experiment Station Bulletin 681. 9 pp.
- Pemberton, R. W. and N. J. Vandenberg. 1993. Extrafloral nectar feeding by ladybird beetles (Coleoptera: Coccinellidae). *Proceedings of the Entomological Society of Washington* 95: 139-151.
- Pimentel, D. 1961. Competition and the species-per-genus structure of communities. *Annals of the Entomological Society of America* 54: 323-333.
- Pimentel, D., C. Glenister, S. Fast, and D. Gallahan. 1984. Environmental risks of biological pest controls. *Oikos* 42: 283-290.
- Pimentel, D. and A. G. Wheeler, Jr. 1973. Species and diversity of arthropods in the alfalfa community. *Environmental Entomology* 2: 659-668.
- Procter, W. 1946. *Biological Survey of the Mount Desert Region. Part VII. The Insect Fauna*. Wistar Institute of Anatomy and Biology, Philadelphia. 566 pp.
- Prokrym, D. R., D. J. Nelson, L. A. Wood, and C. J. Copeland. 1992. Russian wheat aphid biological control project: FY 1992 project report. U.S. Department of Agriculture, National Biological Control Laboratory, Niles, Mich. 55 pp.
- Putman, W. L. 1957. Laboratory studies on the food of some coccinellids (Coleoptera) found in Ontario peach orchards. *Canadian Entomologist* 89: 572-579.
- . 1964. Occurrence and food of some coccinellids (Coleoptera) in Ontario peach orchards. *Canadian Entomologist* 96: 1149-1155.

- Rice, M. E. 1992. High altitude occurrence and westward expansion of the seven-spotted lady beetle, *Coccinella septempunctata* (Coleoptera: Coccinellidae), in the Rocky Mountains. *Coleopterists Bulletin* 46: 142–143.
- Richerson, J. V. and C. J. DeLoach. 1973. Seasonal abundance of *Perilitus coccinellae* and its coccinellid hosts and degree of parasitism in central Missouri. *Environmental Entomology* 2: 138–141.
- Root, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs* 43: 95–124.
- Samways, M. J. 1988. Classical biological control and insect conservation: Are they compatible? *Environmental Conservation* 14: 349–354, 348.
- Schaefer, P. W. and R. J. Dysart. 1988. Palearctic aphidophagous coccinellids in North America, pp. 99–103. *In* Niemczyk, E. and A. F. G. Nixon, eds., *Ecology and Effectiveness of Aphidophaga*. SPB Academic Publishing, The Hague.
- Schaefer, P. W., R. J. Dysart, and H. B. Specht. 1987. North American distribution of *Coccinella septempunctata* (Coleoptera: Coccinellidae) and its mass appearance in coastal Delaware. *Environmental Entomology* 16: 368–373.
- Schooley, H. O., J. W. E. Harris, and B. Pendrel. 1984. *Adelges piceae* (Ratz.), balsam woolly adelgid (Homoptera: Adelgidae). Pp. 229–234. *In* Kelleher, J. S. and M. A. Hulme, eds., *Biological Control Programmes against Insects and Weeds in Canada 1969–1980*. Commonwealth Agricultural Bureaux, Farnham Royal, Slough, England.
- Seibels et al. 1963. Lady beetles-ALABAMA. United States Department of Agriculture, Cooperative Economic Insect Report 13(21): 564.
- Sengonca, C. and B. Frings. 1985. Interference and competitive behaviour of the aphid predators, *Chrysoperla carnea* and *Coccinella septempunctata* in the laboratory. *Entomophaga* 30: 245–251.
- Shade, R. E., H. L. Hansen, and M. C. Wilson. 1970. A partial life table of the cereal leaf beetle, *Oulema melanopus*, in northern Indiana. *Annals of the Entomological Society of America* 63: 52–59.
- Shands, W. A., G. W. Simpson, and M. H. Brunson. 1972. Insect predators for controlling aphids on potatoes. 1. In small plots. *Journal of Economic Entomology* 65: 511–514.
- Simberloff, D. 1992. Conservation of pristine habitats and unintended effects of biological control, pp. 103–117. *In* Kauffman, W. C. and J. R. Neebols, eds., *Selection Criteria and Ecological Consequences of Importing Natural Enemies*. Thomas Say Publications in Entomology: Proceedings. Entomological Society of America, Lanham, Md.
- Smith, B. C. 1958. Notes on relative abundance and variation in elytral patterns of some common coccinellids in the Belleville district. *Annual Report of the Entomological Society of Ontario* 88: 59–60.
- Smith, B. C. 1966. Variation in weight, size, and sex ratio of coccinellid adults (Coleoptera: Coccinellidae). *Canadian Entomologist* 98: 639–644.
- Smith, B. C. 1971. Effects of various factors on the local distribution and density of coccinellid adults on corn (Coleoptera: Coccinellidae). *Canadian Entomologist* 103: 1115–1120.
- Smith, J. B. 1910. Report of the Insects of New Jersey. Annual Report of the New Jersey State Museum, pp. 15–888. MacCrellish & Quigley, Trenton, N.J.
- Soulé, M. E. 1990. The onslaught of alien species, and other challenges in the coming decades. *Conservation Biology* 4: 233–239.
- Sparks, A. N., H. C. Chiang, C. C. Burkhardt, M. L. Fairchild, and G. T. Weekman. 1966. Evaluation of the influence of predation on corn borer populations. *Journal of Economic Entomology* 59: 104–107.
- Staines, C. L., Jr., M. J. Rothschild, and R. B. Trumble. 1990. A survey of the Coccinellidae (Coleoptera) associated with nursery stock in Maryland. *Proceedings of the Entomological Society of Washington* 92: 310–313.
- Stehr, W. C. 1930. The Coccinellidae (ladybird beetles) of Minnesota. University of Minnesota Agricultural Experiment Station Technical Bulletin 75. 54 pp.
- Stoetzel, M. B. 1987. Information on and identification of *Diuraphis noxia* (Homoptera: Aphididae) and other aphid species colonizing leaves of wheat and barley in the United States. *Journal of Economic Entomology* 80: 696–704.
- Sutherland, D. W. S. 1966. Biological investigations of *Trichoplusia ni* (Hübner) and other Lepidoptera damaging cruciferous crops on Long Island, New York. Cornell University Agricultural Experiment Station Memoir 399. 99 pp.
- Swan, L. A. 1964. *Beneficial Insects*. Harper & Row. 429 pp.
- Swan, L. A. and C. S. Papp. 1972. *The Common Insects of North America*. Harper & Row, New York. 750 pp.
- Taylor, T. H. C. 1955. Biological control of insect pests. *Annals of Applied Biology* 42: 190–196.
- Tedders, W. L. 1992. Current trends in insect control: Nuts, Georgia, pp. 256–257. *In* 1992 Insect Control Guide. Meister Publishing Co., Willoughby, Ohio.
- Tedders, W. L. and G. W. Angalet. 1981. Colonization of *Coccinella septempunctata* (L.) in Georgia. *Journal of the Georgia Entomological Society* 16: 47–53.
- Thompson, W. R. and F. J. Simmonds. 1965. A Catalogue of the Parasites and Predators of Insect Pests. Section 4. Host Predator Catalogue. Com-

- monwealth Agricultural Bureaux, Farnham Royal, Bucks, England. 198 pp.
- Travis, J. W., L. A. Hull, and J. D. Miller. 1978. Toxicity of insecticides to the aphid predator *Coccinella novemnotata*. *Environmental Entomology* 7: 785-786.
- Tugwell, P., E. P. Rouse, and R. G. Thompson. 1973. Insects in soybeans and a weed host (*Desmodium* sp.). University of Arkansas Agricultural Experiment Station Report Series 214, pp. 3-18.
- Turnbull, A. L. and D. A. Chant. 1961. The practice and theory of biological control of insects in Canada. *Canadian Journal of Zoology* 39: 697-753.
- U.S. Congress, Office of Technology Assessment. 1993. Harmful Non-Indigenous Species in the United States. OTA-F-565. U.S. Government Printing Office, Washington, D.C. 391 pp.
- van den Bosch, R. and K. S. Hagen. 1966. Predaceous and parasitic arthropods in California cotton fields. University of California Agricultural Experiment Station Bulletin 820. 32 pp.
- van den Bosch, R. and A. D. Telford. 1964. Environmental modification and biological control, pp. 459-488. In DeBach, P., ed., *Biological Control of Insect Pests and Weeds*. Chapman and Hall, London.
- Webb et al. 1965. Lady beetles—ALABAMA. United States Department of Agriculture, Cooperative Economic Insect Report 15(22): 556.
- Weiss, H. B. and E. L. Dickerson. 1919. Insects of the swamp rose-mallow, *Hibiscus moscheutos* L., in New Jersey. *Journal of the New York Entomological Society* 27: 39-68.
- Weiss, H. B. and E. L. Dickerson. 1921. Notes on milkweed insects in New Jersey. *Journal of the New York Entomological Society* 29: 123-145.
- Wheeler, A. G., Jr. 1989. *Cinara pilicornis* (Hartig), a pest of nursery-grown spruce. *Regulatory Horticulture* 15(2): 13-15.
- . 1993. Establishment of *Hippodamia variegata* and new records of *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae) in the eastern United States. *Entomological News* 104: 102-110.
- Wheeler, A. G., Jr. and E. R. Hoebeke. 1985. The insect fauna of ninebark, *Physocarpus opulifolius* (Rosaceae). *Proceedings of the Entomological Society of Washington* 87: 356-370.
- Wheeler, A. G., Jr. and J. F. Stimmel. 1979. Bean aphid on ornamental euonymus: seasonal history and damage. *Melsheimer Entomological Series* 27: 26-29.
- . 1983. The phytophagous and predacious arthropod fauna of soybean in Pennsylvania. *Melsheimer Entomological Series* 33: 31-38.
- Whitcomb, W. H. and K. Bell. 1964. Predaceous insects, spiders, and mites of Arkansas cotton fields. University of Arkansas Agricultural Experiment Station Bulletin 690. 84 pp.
- Wingo, C. W. 1952. The Coccinellidae (Coleoptera) of the Upper Mississippi Basin. *Iowa State Journal of Science* 27: 15-53.
- Wright, E. J. and J. E. Laing. 1980. Numerical response of coccinellids to aphids in corn in southern Ontario. *Canadian Entomologist* 112: 977-988.
- Yadava, C. P. and F. R. Shaw. 1968. The preferences of certain coccinellids for pea aphids, leafhoppers, and alfalfa weevil larvae. *Journal of Economic Entomology* 61: 1104-1105.
- Zim, H. S. and C. Cottam. 1956. *Insects: A Guide to Familiar American Insects*. Golden Press, New York. 160 pp.
- Zwölfer, H. and P. Harris. 1971. Host specificity determination of insects for biological control of weeds. *Annual Review of Entomology* 16: 159-178.